INTERACTIVE EFFECTS OF DISTURBANCE AND DISPERSAL ON COMMUNITY ASSEMBLY

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INTERACTIVE EFFECTS OF DISTURBANCE AND DISPERSAL ON COMMUNITY ASSEMBLY

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SUMMARY

The traditional debate on alternative community states has been over whether or not they exist. Recent studies have focused on the role of assembly history in dictating community divergence, but the context in which assembly history becomes important is a continued topic of interest. In this study, we created communities of bacterivorous ciliated protists in laboratory microcosms and manipulated assembly history, disturbance frequency, and the presence of dispersal among local communities to investigate the mechanisms behind community divergence. Specifically, we sought to understand how the role of assembly history changed in response to disturbance, dispersal, and the combination of the two**.** Assembly history determined the identity of the dominant species through priority effects, and dispersal and disturbance showed interactive effects on both alpha and beta diversity. Dispersal increased alpha diversity, but only in the absence of disturbance, and it reduced beta diversity, but not in the presence of low or mixed disturbance treatments. These results show that the role of assembly history and the strength of priority effects are dependent on community context. Each factor cannot be viewed in isolation, and understanding the interaction between them is important for understanding how communities assemble, which lends insight into how ecological restoration should be approached.

CHAPTER 1

INTRODUCTION

With the sudden collapse of critical ecosystems such as kelp beds (Estes and Duggins 1995), coastal ecosystems (Jackson et al. 2001), and coral reefs (Knowlton 1992, Hughes 1994), the concept of alternative community states has been a topic of substantial interest in the field of ecology. This concept suggests that there can be more than one community state that differs in species composition and abundance under the same environmental conditions and species pools, and that once a community reaches an alternative state, it does not change unless it is disturbed beyond a certain threshold point (Lewontin 1969, Sutherland 1974, May 1977, Holling 1995, Mumby et al. 2007). Since its introduction, numerous theoretical and empirical studies in both aquatic and terrestrial systems have been documented (reviewed by Beisner et al. 2003, Schröder et al. 2005).

Historically, research on alternative community states has been focused on single factors, largely owing to the fact that the processes that shape alternative community states is difficult to observe within appropriate temporal and spatial scales (Connell and Sousa 1983). However, one of the major goals of community ecology is to understand how multiple processes combine to produce the patterns of species abundances, distributions, and diversity. The focus of some recent research and this study is on understanding the mechanisms involving multiple factors that produce divergent communities.

One of the key determinants of community structure is assembly history (Diamond 1975, Loreau et al. 2001, Chase 2003, Chase 2007, Jiang and Patel 2008, Jiang

et al. 2011b, Fukami 2015). Diamond (1975) was one of the first to observe in island habitats that community structure seemed to vary depending on the order of species invasions, hypothesizing that the prior colonizers would influence the success of the latter colonizers. Subsequent theoretical and empirical studies showed that changing the initial species composition could cause the communities to have divergent species compositions at the end of assembly (e.g., Law and Morton 1993, Inouye and Tilman 1995, Suding et al. 2004, Fukami et al. 2005, Fukami and Nakajima 2013). Experimentation since then, such as the study with laboratory microcosms by Jiang et al. (2011b), showed that the effect of assembly history could display itself through priority effects, or the effect species have on one another, depending on the order in which they arrive at a site (Fukami 2015). Priority effects can operate under two mechanisms: niche preemption and niche modification. Niche preemption occurs when prior colonizers reduce the amount of resources available for later colonizers and thereby inhibit colonization by later arriving species (Chesson 2000). On the other hand, niche modification occurs when prior colonizers alter the types of niches available for the later colonizers to occupy (Peterson 1984).

However, some theoretical models such as the study by Law and Morton (1996) and controlled experiments (Neill 1975, Tilman et al. 1986, Sommer 1991) show that history could have minimal or no effect on community structure. The microcosm study by Jiang et al. (2011b) also shows that random events could drive community structure, suggesting that assembly history may not always be important. In that study, community divergence did not occur at random, but rather seemed to depend on the levels of productivity, suggesting that certain communities are more sensitive to the effect of

assembly history than others. As also seen in a survey of freshwater ponds by Chase (2003), the role of assembly history in the formation of alternative community states is dependent on other factors.

Previous studies show that dispersal is one such factor (as reviewed by Cadotte 2006). Dispersal is predicted to increase local species richness, or alpha diversity, by offsetting species loss from competition caused extinctions, as extinction prone populations are subsidized from larger, more secure populations (Chase 2003, Cadotte et al. 2006, Mouquet and Loreau 2003). Too much dispersal, however, may reduce alpha diversity if it results in the regional dominance of the same competitors (Mouquet and Loreau 2003). While assembly history can lead to the exclusion of later colonizers through priority effects in closed systems (Loreau and Mouquet 1999), dispersal between communities can increase the likelihood for local coexistence through the source-sink effect and the regional compensation of local competitive abilities, resulting in decreased beta diversity (Mouquet and Loreau 2003, Cadotte and Fukami 2005). A theoretical study by Shurin et al. (2004) also shows that dispersal among local communities may make it difficult to maintain historical contingency. On the other hand, Pu and Jiang (2015) found in a protist microcosm experiment that dispersal did not reduce historical contingency even with high rates of dispersal, suggesting that the role of dispersal may also be context dependent.

In addition to dispersal, disturbance can also alter the role of assembly history. Disturbance resets or alters the community composition by killing or damaging resident species and allowing new colonizers to enter the community. Higher disturbance is expected to reduce historical contingency as it may reduce the competition from

disturbed resident communities on new colonizers (Chase 2003). Consistent with this idea, Jiang and Patel (2008) found that increasing disturbance tended to reduce beta diversity in bacterivorous protist communities, suggesting the reduced likelihood of alternative community states under greater disturbance. Likewise, Chase (2007) reported that increased disturbance and harsher environments caused freshwater pond communities to become more similar as niche selection filtered out species from the regional species pool that could not tolerate the given environment.

While there have been studies that examine the individual effect of disturbance and dispersal on community assembly, how the two combine to affect community assembly has rarely been tested. A recent study by Vanschoenwinkel et al. (2013) tested how both dispersal and disturbance structure rock pool invertebrate metacommunities. They found that communities with higher disturbance were more sensitive to the effects of dispersal, and that dispersal compensated for the negative effects of disturbance. On the other hand, an experiment with freshwater microzooplankton by Östman et al. (2006) did not find a significant interaction between disturbance and dispersal on local species richness. Neither study, however, directly manipulated assembly history. More generally, despite the growing number of studies that examine the factors that regulate the formation of alternative community states, the context in which assembly history becomes relevant is still understudied (Fukami 2015). Therefore, rather than asking whether alternative community states exist, the goal of our study is to determine the circumstances, concerning disturbance and dispersal, under which assembly history promotes community divergence.

In this study, we report, to our knowledge, the first experiment that directly manipulated assembly history, disturbance, and dispersal to investigate their potential interactive effects on the formation of alternative community states. In our experiment, we used bacterivorous protists as our model organisms, introduced them in different colonization sequences, and manipulated disturbance and dispersal frequencies. We used bacterivorous ciliated protists with short generation times ranging from 8-39 hours, which enabled observations over numerous generations (about 80 days), strict controls, and replication (Thrasher and Adams 1972, Finlay 1977, Twagilimana et al. 1998). Although microcosm studies sacrifice natural context (Carpenter 1996), using microcosms enabled us to minimize the transient dynamics that may complicate the interpretation of alternative community states (Connell and Sousa 1983).

CHAPTER 2

MATERIALS AND METHODS

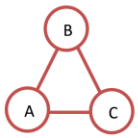
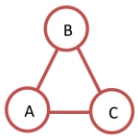
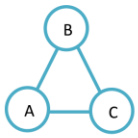
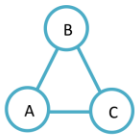
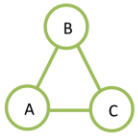
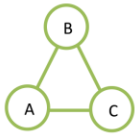
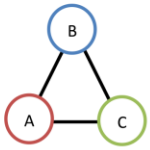
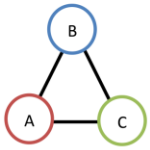
Five bacterivorous protists species were used in the experiment: *Paramecium bursaria, Paramecium caudatum, Spirostomum teres, Colpidium kleini,* and *Tetrahymena pyriformis*. These five species were chosen because of their morphological distinctness and varying degrees of competitive ability (Violle et al. 2010). These species were isolated from freshwater ponds or purchased from Carolina Biological Supply (Burlington, North Carolina, USA), and cultured in the lab for many generations prior to this experiment. Stock cultures were prepared from these cultures in 250mL autoclaved glass jars. Each jar was filled with 100mL of growth medium, prepared by mixing 0.55g of protozoan pellet (Carolina Biological Supply, Burington, NC, USA) per 1L of deionized water; stock cultures were maintained for two weeks prior to the start of the experiment. The medium was first inoculated with species of bacterial prey (*Bacillus cereus, Bacillus subtilis,* and *Serratia marcescens)*. To prepare the bacterial inoculum, stock cultures from all protist species were mixed together, and then filtered to remove the protists. The bacterialized medium was distributed into each microcosm 24 hours after inoculation. To provide an additional source of carbon, two autoclaved wheat seeds were added to each stock culture.

The microcosms used in this experiment were created in a similar manner in 250mL autoclaved glass jars, 100mL of medium inoculated with bacterial prey, and two wheat seeds. All stock cultures and microcosms were stored in an incubator maintained at 22℃ under 24 hours of light. Each week, 7% of medium from each microcosm was

replaced with fresh autoclaved medium to replenish nutrients and to remove metabolic wastes. Previous studies with protist microcosms show that weekly medium replacement of this magnitude does not have a significant effect on community dynamics (Jiang et al. 2011a).

For this experiment, we used a 4 x 2 x 3 factorial design with four disturbance frequency treatments and two dispersal treatments, repeated over three different assembly histories (summarized in Table 1). Each treatment combination was repeated three times for a total of 72 microcosms. Each metacommunity consisted of three microcosms, each with a different assembly history.

Table 1. Experimental Setup. Weekly dispersal was either absent (0) or present (1). There were three disturbance treatments: absent (N), biweekly (L), weekly (H), and mixed (M). There were three assembly history sequences (A, B, C), and three replicates for a total of 72 microcosms. *Note:* See Table 2 for introduction order of protists for each assembly history sequence.

		Dispersal	
Assembly Histories: A, B, C		Absent (Control)	Present (Once every week)
Disturbance	Absent (Control)		
	Low Frequency (Once every 2 weeks)		
	High Frequency (Once every week)		
	Mixed (Red - 0, Blue - 1/wk, Green - 1/2wks)		

For sequential community assembly, we had three sequences: A, B, and C. The order of protist species introduction was determined by random draws from the species pool (assembly sequences summarized in Table 2). Every seven days, 100 individuals of a new species were added to each jar until all five protist species were introduced. As a control, one assembly sequence (sequence A) had all five protist species simultaneously introduced into microcosms at the same time. Two weeks before a species was introduced, a new stock culture of the species was created to ensure that individuals introduced into the experimental microcosms at different times were the same age and in similar physiological states.

Table 2. Community Assembly Sequences used in this experiment.

Week	Sequence A: Control	Sequence B	Sequence C
1	All species	*Paramecium bursaria*	*Tetrahymena pyriformis*
2		*Spirostomum teres*	*Spirostomum teres*
3		*Paramecium caudatum*	*Paramecium bursaria*
4		*Tetrahymena pyriformis*	*Colpidium kleini*
5		*Colpidium kleini*	*Parmecium caudatum*

There were four disturbance levels: an undisturbed control (N), a biweekly disturbance (L), a weekly disturbance (H), and a mixed disturbance (M) regime. Each microcosm within the same metacommunity was subject to the same disturbance treatment, except for the mixed disturbance in which one of the microcosms was undisturbed, the second was disturbed biweekly, and the third was disturbed weekly (Table 1). Due to logistic constraint, only one disturbance-history combination was used in this mixed disturbance treatment. Disturbance was imposed through sonication using a

Sonic Dismembrator Model 150 (Fisher Scientific, Waltham, Massachusetts, USA), which subjected the microcosms to indiscriminate density-independent mortality. Each microcosm was subjected to sonication at 50% power for 10 seconds. Unlike a previous microcosm study by Jiang and Patel (2008), disturbance regimes here were manipulated by changing the frequency, as opposed to intensity.

Dispersal was either absent (0) or present (1). For treatments with dispersal, it was simulated by taking 7% of medium from each of the three microcosms in a metacommunity, mixing it, and evenly redistributing the mixed medium back into each microcosm. The 7 mL of medium was taken from each microcosm to simulate a rate of dispersal that is relatively high for protists and other zooplankton in hydraulically connected ponds in the field (Michels et al. 2001).

Weekly sampling was conducted over a period of 10 weeks, and the population density of each protist species (in the unit of individuals per mL) was recorded. For each sample, we took ~0.3 mL of medium from each microcosm, distributed it into small drops on a pre-weighted Petri dish, weighed the sample with an analytic balance, and counted the number of individuals of each protist species under a microscope.

Statistical analyses were performed using R v. 3.0.2 (www.r-project.org). The effects of disturbance, dispersal, and assembly history on species richness (α diversity) in local communities on the last sampling day were assessed using a three-way ANOVA. We calculated β diversity, averaged for each metacommunity, with the commonly used Bray-Curtis Index of Dissimilarity based on data collected from the last sampling day, and assessed the effects of disturbance and dispersal on β diversity using a two-way ANOVA. Community divergence was further examined using a principal component

analysis (PCA), based on the protist abundances on the last sampling day. The strength of priority effects was assessed using the Pearson's correlation test and regression analyses (Pu and Jiang 2015).

CHAPTER 3

RESULTS

Alpha Diversity

Based on data from the last sampling day, ANOVA results showed that the interaction between dispersal and disturbance on species richness was significant (Three-Way ANOVA, Table 3, $F(3,69) = 3.25$, $p = 0.022$). Post-hoc Tukey analyses revealed that alpha diversity values were not significantly different between disturbance treatments in the presence of dispersal, with the exception of communities with the treatment combination no disturbance / with dispersal / assembly sequence A (N1A), in which alpha diversity was lower (Figure 1). The significant interaction between dispersal and disturbance was largely driven by the fact that in the absence of dispersal, the treatment without disturbance had the lowest alpha diversity, but in the presence of dispersal, its values were not significantly different from the other disturbance treatments (Figure 1).

Table 3. Alpha Diversity ANOVA Results. The below table summarizes the results of a three-way ANOVA based on final species richness (alpha diversity) from the last sampling day.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Disturbance	3	0.05674	0.3846	7.560	0.00179	**
Dispersal	1	0.17555	1.0377	12.000	0.00140	**
History	2	0.16050	0.0802	0.240	0.1890	
disturbance:dispersal	3	1.00560	0.3352	3.250	0.0220	*
disturbance:history	6	0.61730	0.1543	1.750	0.1880	
dispersal:history	2	0.25930	0.1296	0.230	0.2023	
disturbance:dispersal:history	4	0.96300	0.2407	3.25	0.0219	*
Residuals	36	3.25982	2.3623			

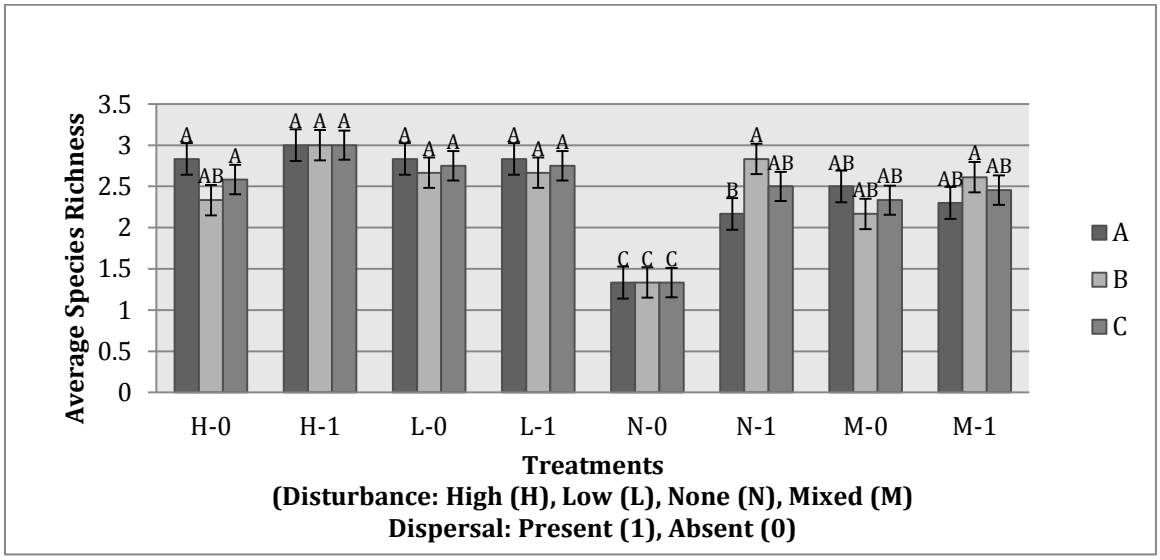


Figure 1. Final Species Richness. Average final species richness ± standard error, based on the last sampling day for each assembly history sequence (A, B, and C) subjected to each disturbance and dispersal treatment combination. Each community had 5 ciliated protist species introduced in different sequences (see Table 2). Communities were subjected to four levels of disturbance (undisturbed, biweekly, weekly, and mixed disturbances) and two levels of dispersal (absent or present). Tukey HSD test results are shown as letters above columns. Bars that do not share the same letter are significantly different from each other.

The interactive effect of all three factors was also significant on species richness (ANOVA, $F(6,68) = 3.25$, $p = 0.0219$). While assembly history had a significant effect on species richness in treatments with high disturbance / no dispersal (H0) and no disturbance / with dispersal (N1), there were no significant differences in alpha diversity values between different assembly histories for the other treatments (Figure 1).

Beta Diversity

Beta diversity was calculated using the Bray-Curtis Index to determine dissimilarity between local communities. In all treatments, beta diversity decreased over time, and in general, final beta diversity was higher in communities without dispersal than communities with dispersal, with the exception of the low and mixed disturbance treatments (Figure 2, 3). In the absence of dispersal, all treatments maintained relatively high dissimilarity until week six of the experiment, as not all five protist species were present in communities with sequences B and C until week five (Figure 2).

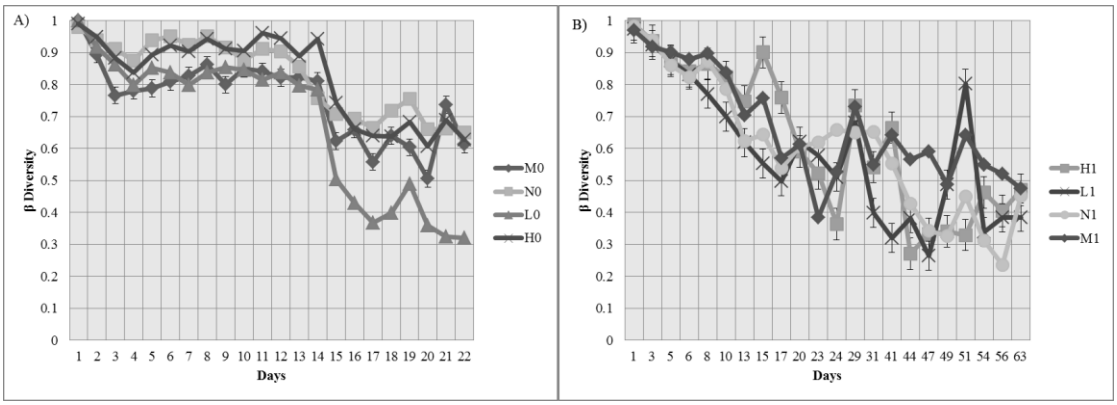


Figure 2. Average Beta Diversity Over Time. Average beta diversity, calculated by the Bray-Curtis Index ± standard error among communities subjected to different disturbance treatments A) without dispersal and B) with dispersal through time. Each community had 5 ciliated protist species introduced in different sequences (see Table 2). Communities were subjected to four levels of disturbance (undisturbed (N), biweekly (L), weekly (H), and mixed (M) disturbances) and two levels of dispersal (present (1) and absent (0)).

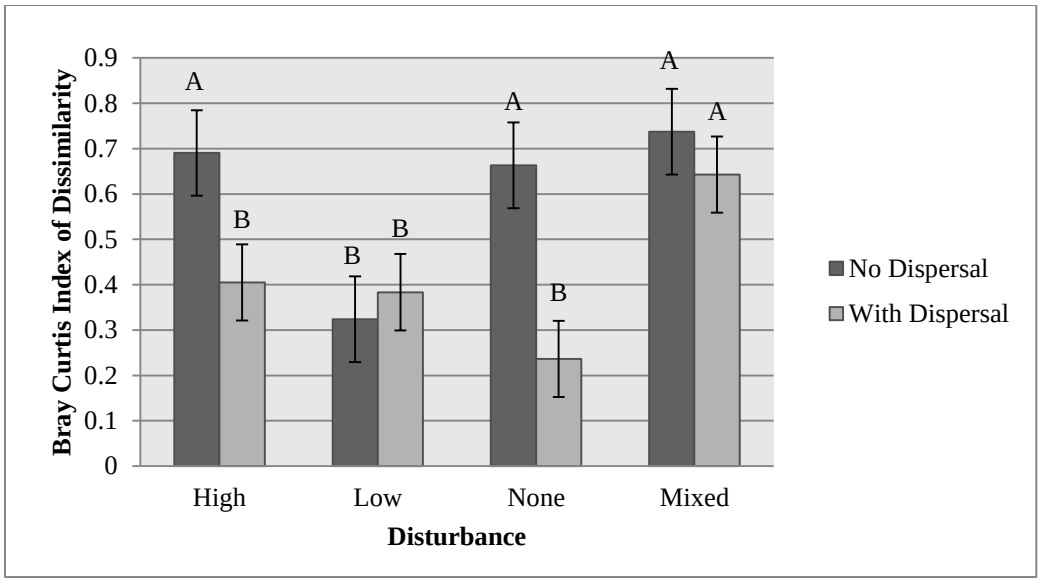


Figure 3. Final Beta Diversity. Average final beta diversity from the last sampling day ± standard error, calculated using the Bray-Curtis Index for each treatment Tukey HSD test results are shown as letters above columns. Bars that do not share the same letter are significantly different.

ANOVA results show that while disturbance did not have a significant main effect on beta diversity, dispersal and the interaction between the two had a significant effect on the final beta diversity values (Table 4). While beta diversity values between dispersal-absent and -present communities in the no and high disturbance treatments (N0/N1, H0/H1) were significantly different, there was no significant difference between the two dispersal treatments under low or mixed disturbance (Figure 2), resulting in the significant interactive effect of dispersal and disturbance. Interestingly, the beta diversity for the low disturbance frequency treatment decreased significantly around week six, while that of the other disturbance treatments remained at relatively high levels (Figure 2). The difference in community structure can be seen in the pattern of species abundances depicted in Figure 4, which shows that communities under low disturbance and no dispersal were the only ones with three species present across all assembly histories,

while other treatments varied between two species and three species present, depending on the assembly history. Communities with low disturbance and no disturbance had stable populations of *P. bursaria, C. kleini,* and *T. pyriformis* (Appendix A-C).

Table 4. Beta Diversity ANOVA Results. Two-way ANOVA based on Bray-Curtis Index of Dissimilarity between local communities on the last sampling day.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
disturbance	3	0.05674	0.01891	1.526	0.233267	
dispersal	1	0.17555	0.17555	14.166	0.000955	***
disturbance:dispersal	3	0.15003	0.05001	4.035	0.018603	*
Residuals	24	0.29743	0.01239			

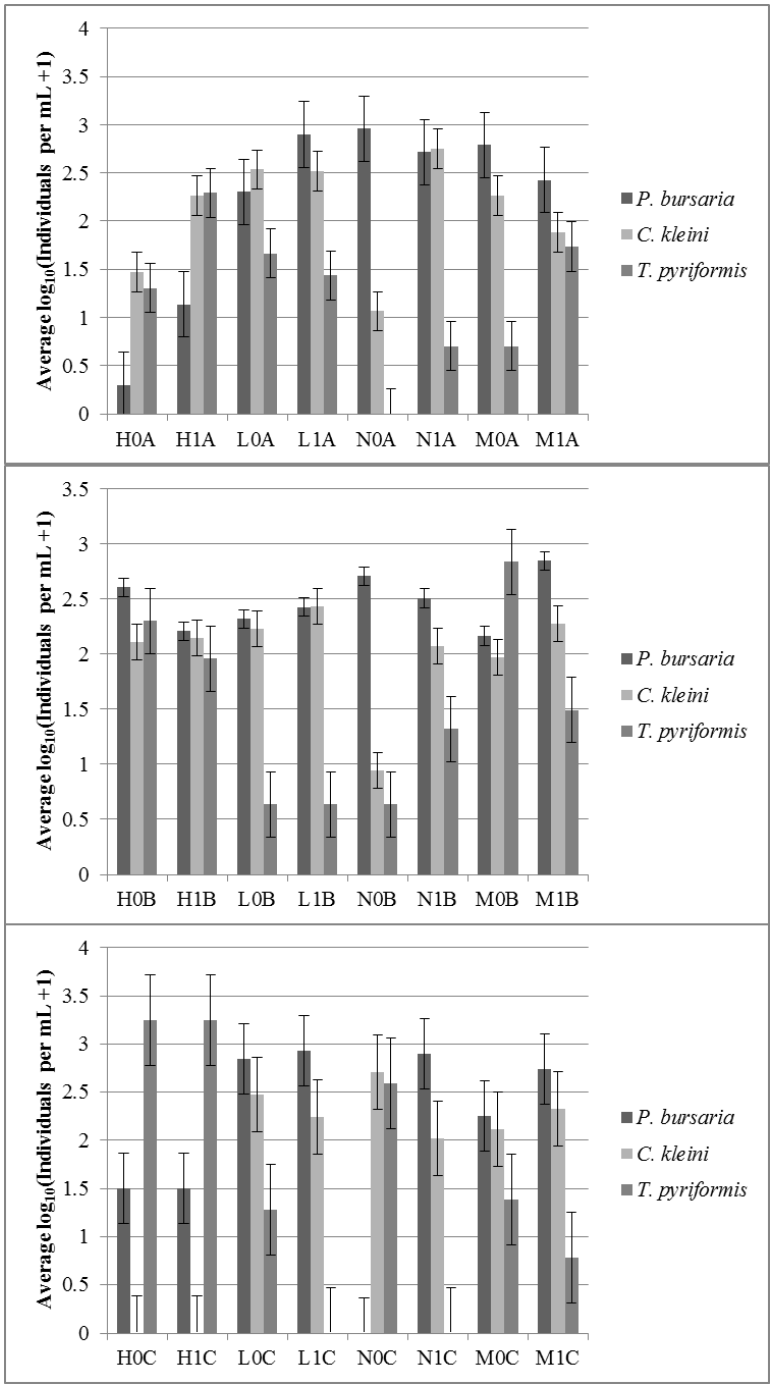


Figure 4. Absolute Abundances in Final Community State. Final average abundances in final community state per species for each treatment from the last sampling day are shown for each disturbance, dispersal, and assembly history combination. Abundances shown are log transformations of actual population densities per mL of medium. Error bars represent standard error.

The results of the principal component analysis (PCA) are summarized in Figure 5 and Table 5. PCA shows that there were two principal components that together explained 90% of the variance, and a third component that explained 9.9% of the variance. The first PC component explained 64.6% of the variance, showing the contrast between communities with high abundance of *P. bursaria* and communities with high abundance of *T. pyriformis* (Figure 5). The second PC component showed the contrast between communities with *P. bursaria* and *T. pyriformis,* and communities with *C. kleini*, which explained 25.4% of the variation (Figure 5). When the main clusters were compared, one of the clusters that formed had communities with treatment combinations of high disturbance, assembly history C, with and without dispersal (H1C, H0C), which was dominated by *T. pyriformis*, while a second cluster, such as the community with treatment combination no disturbance / no dispersal / sequence A (N0A), consisted mainly of communities dominated by *P. bursaria* (Figures 4, 5). There was a third cluster that contained communities that were dominated by both *C. kleini* and *P. bursaria*.

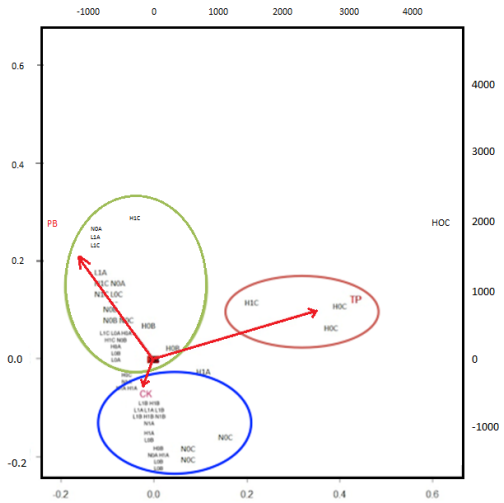


Figure 5. Principal Component Analysis of Protist Communities. Each three-letter and number combination corresponds to a community. Letters N, L, H, and M denote the undisturbed, biweekly, weekly, and mixed disturbance treatments respectively. Dispersal is denoted by numbers 0 (absent) and 1 (present), and letters A, B, and C denotes assembly history sequences. Clusters are indicated by the blue, green, and red circles.

Table 5. Principal Component Analysis Loadings. Species names and their abbreviations are as follows: *Paramecium* bursaria (PB), *Paramecium caudatum* (PC), *Spirostomum teres* (ST), *Colpidium kleini* (CK), and *Tetrahymena pyriformis* (TP). Note that blank entries are small, but not zero.

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
PB	-0.43	0.885	0.178		
PC				0.995	0.102
ST				-0.102	0.995
CK		-0.227	0.972		
TP	0.901	0.406	0.154		

Individual Species Patterns

Among the protist species that were used in this experiment, two (*Paramecium caudatum* and *Spirostomum teres*) went extinct in all communities. Abundance graphs indicate three possible community outcomes, which is consistent with the clusters formed

by the PCA (Figure 4, 5). One possible outcome is a community in which *Paramecium bursaria* dominated the community, a second in which *Tetrahymena pyriformis* dominated, and a third in which *Colpidum kleini* and *P. bursaria* co-dominated. Pearson correlation tests show that there was not a significant correlation between the introduction order and final abundance for *C. kleini*, but there was a strong positive correlation for *T. pyriformis* ($r(70) = 0.76$, $p = 0.019$) and for *P. bursaria* ($r(70) = 0.56$, $p = 0.022$), indicative of inhibitive priority effects. Further regression analysis revealed that for both *P. bursaria* and *T. pyriformis*, priority effects were strongest in communities with no disturbance and no dispersal (N0), as well as communities with high disturbance and no dispersal (H0). However, the slope was not significant for all other treatments.

CHAPTER 4

DISCUSSION

Studies on alternative community states in the past have been mainly observational or based on a posteriori reasoning, and the traditional debate has been on whether multiple states can exist (as reviewed by Schröder *et al.* 2005). An increasing number of studies have started looking at how assembly history affects community divergence (Chase 2003, Jiang et al. 2011, etc.), and further studies investigated how other factors, such as dispersal (Fukami 2005, Cadotte and Fukami 2005, Pu and Jiang 2015) and disturbance (Trexel et al. 2005, Chase 2007, Jiang and Patel 2008), regulate the role of assembly history in shaping communities. However, further research into the context that determines when communities are sensitive to the effect of assembly history is still much needed (Fukami 2015). In this study, we provide experimentation that explored how disturbance and dispersal, when manipulated together, influence community structure. We found there was a significant interactive effect of dispersal and disturbance on alpha and beta diversity, and consequently on the role of assembly history in influencing community assembly. While assembly history determined the identity of the dominant species through priority effects, dispersal increased alpha diversity, but only in the absence of disturbance. Beta diversity decreased in the presence of dispersal, but only in treatments with no or high levels of disturbance.

The Role of Assembly History

Assembly history had a clear role in community divergence in our experiment. According to the results of the principal component analysis, species abundances were

mainly driven by *P. bursaria* and *T. pyriformis* (Figure 5, Table 5). *P. bursaria* was the strongest competitor in our control assembly sequence (sequence A) because the microcosms had access to light, allowing *Chlorella*, an endosymbiotic and photosynthetic algae, to provide *P. bursaria* with an additional source of energy (Karakashian 1975). *T. pyriformis*, on the other hand, was an inferior competitor that is better able to tolerate disturbance due to its higher growth rates and larger carrying capacities (Violle et al. 2010). In communities with assembly history B, *P. bursaria* was the first species to colonize the community, and a significant correlation between its order of introduction and final abundance suggests that priority effects contributed to its dominance. However, *P. bursaria* did not dominate in communities with assembly history C, in which the inferior competitor, *T. pyriformis*, first colonized the communities. There was a strong correlation between colonization order and final abundance for *T. pyriformis*, indicating that prior colonization may have allowed *T. pyriformis* to establish dominance through priority effects, despite it being a weaker competitor.

Interaction between Disturbance and Dispersal: Alpha Diversity

Our results show that the role of assembly history changed depending on the presence of disturbance and dispersal, which had an interactive effect on both alpha and beta diversity. While previous studies predict that communities with dispersal have higher alpha diversity (Mouquet and Loreau 2003, Cadotte et al. 2006), we found this was true only in undisturbed communities. These disturbance-free communities displayed source-sink dynamics in the presence of dispersal. For example, in communities with Assembly A and without dispersal, *P. bursaria* tended to dominate, and the *T. pyriformis* population gradually decreased and was extinct by week 8. With dispersal, the extinction

of *T. pyriformis* and *C. kleini* was prevented through the immigration of individuals from communities with assembly C (Appendix A, C). Previous empirical studies show that such source-sink dynamics, caused by differences in assembly history in our study, prevent the decline in both abundance and distribution of species (Gonzalez et al. 1998, Shurin 2001). However, this pattern did not hold true in the presence of disturbance, as all three species were able to coexist locally. One possible explanation for this result is the tradeoff *P. bursaria* has between competitive ability and disturbance tolerance. Previous experimentation by Violle et al. (2010) showed that *P. bursaria,* compared to *T. pyriformis* and *C. kleini,* is a better competitor, but less tolerant of disturbance. Our results also show that *P. bursaria* populations tend to decrease with higher disturbance (Figure 5). Consequently, high disturbance may have prevented the dominance of *P. bursaria* and allowed for the persistence of more disturbance tolerant populations of *T. pyriformis* and *C. kleini*.

Notably, despite this competitive ability and disturbance tolerance tradeoff, our results did not lend support to the intermediate hypothesis (IDH), which predicts that alpha diversity is highest at intermediate levels of disturbance (Connell 1978). Although our results show that there were differences in community structure in response to disturbance treatments, the IDH did not hold true as alpha diversity was not significantly different between disturbance treatments (Figure 1). One possible reason for this deviation is because priority effects, rather than disturbance level, strongly influenced species richness. For example in communities with high disturbance, no dispersal, and sequential assembly (H0B, H0C), three species were present and *P. bursaria* dominated with sequence B, but with sequence C, only two species were present and *T. pyriformis*

dominated. In addition to priority effects, the mixed disturbance treatment provides another possible reason for this discrepancy. In both the presence and absence of dispersal, the mixed disturbance treatment, having patches with different disturbance levels, allowed the disturbance intolerant species refuge and consequently coexistence within the community, showing that the spatial scale at which communities are disturbed also affects diversity patterns (Chase 2003, Östman et al. 2006).

Interaction between Disturbance and Dispersal: Beta Diversity

Consistent with a modeling study by Shurin et al. (2004), we found that dispersal reduced beta diversity for communities with high disturbance and no dispersal (Figure 2A, 3). However, our results were contrary to a previous study by Pu and Jiang (2015), which found that dispersal did not reduce historical contingency in protist microcosms. Two factors could contribute to this discrepancy. Firstly, our system only had three species remaining in the final community, while Pu and Jiang (2015) had six. With only three species remaining, the possible community outcomes were comparatively limited. A second factor may be the difference in dispersal rates. Our dispersal rates were significantly higher at 7%, while the highest dispersal rate used by Pu and Jiang (2015) was at 5%. Our higher dispersal rate may have reduced beta diversity through mass effects.

However, we also found that dispersal did not reduce beta diversity under low and mixed disturbance (Figure 2A, 4), demonstrating the interactive effects of disturbance and dispersal on beta diversity. As expected, undisturbed treatments had higher beta diversity than low disturbance treatments in the absence of dispersal (Chase 2003, Chase 2007, Jiang and Patel 2008). However, the presence of dispersal among low disturbance

communities did not reduce beta diversity further. Rather, beta diversity was the lowest for low disturbance treatments, and not significantly different between treatments with and without dispersal (Figure 3). For treatments with low disturbance, *P. bursaria* and *C. kleini* were equally dominant, regardless of dispersal (Figure 4), suggesting that low disturbance allowed for their coexistence. Based on regression analysis results, priority effects were not detected in low disturbance communities, both with and without dispersal, suggesting that deterministic processes dictated community structure. Lepori and Malmqvist (2009) observed in a study on macroinvertebrate communities in mountain streams that for low disturbance treatments the relative importance of deterministic and stochastic processes was dependent on the disturbance level. In that study, streams with low levels of flood disturbance tended to have the lowest beta diversity as stochastic processes were suppressed, and deterministic niche selection caused rare species to be filtered out, reducing the size of the colonizer pool (Lepori and Malmqvist 2009). Similarly in our study, in the absence of priority effects, disturbance apparently overwhelmed the effect of dispersal, and ultimately governed species patterns in these treatments.

We also found that in the absence of dispersal, high disturbance did not reduce beta diversity (i.e. the role of assembly history) as expected (e.g. Trexel et al. 2005, Chase 2007, Jiang and Patel 2008). One possible factor that contributed to this result is the lower total abundance in communities with Assembly A, causing those communities to be distinct from those with Assembly B and C (Figure 5). Violle et al. (2010) found in an experimental study on protist species that increased disturbance made each species more vulnerable to disturbance due to reduced population densities. The increased

vulnerability to disturbance, the absence of priority effects (as all species were introduced simultaneously in Assembly A), and the lack of dispersal may have caused the abundances in these communities to be significantly reduced.

Beta diversity values in the mixed disturbance treatment were also contrary to expectations. The metacommunity that was subject to the mixed disturbance treatment had three local communities each subject to different levels of disturbance, creating abiotic environmental heterogeneity. While we expected that in the presence of dispersal, beta diversity for the mixed disturbance treatments would also be low due to source-skink dynamics, results show that beta diversity was still high. Furthermore, unlike communities with high or no disturbance, beta diversity was not significantly different between treatments with and without dispersal (Figure 3). Apparently, different levels of disturbance within our metacommunities created environmental heterogeneity among local communities, and allowed for distinct communities to persist through species sorting. In the undisturbed patch, *P. bursaria* dominated, whereas highly disturbed patches were dominated by *T. pyriformis* (Figure 5). A review by Cottenie (2005) showed that species sorting is a highly prevalent process driving metacommunity dynamics, in which the gradient of abiotic factors creates different patches for different species to occupy. Individual species are then separated into different patches, and the effect of dispersal is insufficient to alter their distribution (Leibold et al. 2004). Our results are similar to a study by Van der Gucht et al. (2007), which showed that species sorting largely determined the structure of natural bacterial communities, and suggested that the fast generation time of the study system further contributed to species sorting. We similarly had a study system with fast generation times (8-39 hours), and the mixed

disturbance treatment may have allowed for high beta diversity through species sorting, which overwhelmed any effect that dispersal may have had.

There are only a limited number of studies that look at the interactive effect of dispersal and disturbance on community structure. A previous study on invertebrate rock pool metacommunities by Vanschoenwinkel et al. (2013) also found that there was a significant interaction between dispersal and disturbance, as the combination of increased dispersal and increased disturbance increased alpha diversity, suggesting that communities are more sensitive to effects of dispersal if they are more disturbed. Our results were partially consistent with these findings. Contrary to Vanschoenwinkel et al. (2013), we found that dispersal increased alpha diversity only in the absence of disturbance. However, we did find that beta diversity decreased in high disturbance treatments, but only in the presence of dispersal (Figure 3), suggesting that frequently disturbed communities may be more sensitive to later arriving species, such as invasive species.

Caveats

One of the limitations of this study is that the type of disturbance we experimentally introduced was in the form of indiscriminate sonication. We did not manipulate other forms of disturbance, which, for example, could cause density or size dependent mortality (Huston 1994); these different disturbance regimes should be considered by future experiments of community assembly. Furthermore, because the two largest species, *Paramecium caudatum* and *Spirostomum teres*, went extinct in all treatments of our study, there were only 3 species on which to base species richness and community divergence analyses. A third limitation of this study is that it examines

community structure at a single trophic level, although *P. bursaria* is also capable of autotrophy through its endosymbiont. Few studies have examined the effect of diversity and assembly history across multiple trophic levels on community structure (Duffy et al. 2007). For example, a modeling study based on patterns of phytoplankton, zooplankton, and fish species by Shurin and Allen (2001) showed that dispersal rates of predator species affected diversity patterns, suggesting that the importance of assembly history may change depending on timing of predator or prey arrival. In addition to the inclusions of predators, future work should examine the effects of dispersal, disturbance, and consumer assembly history on prey species and basal resources. Previous microcosm studies show that the assembly history of predator species has long-lasting effects on the abundances of prey (Olito and Fukami 2009). In our study, bacterial species were inoculated into the medium as a basal resource, and bacterial data, which were not collected here, could provide further insight into how consumer community assembly affects prey community assembly.

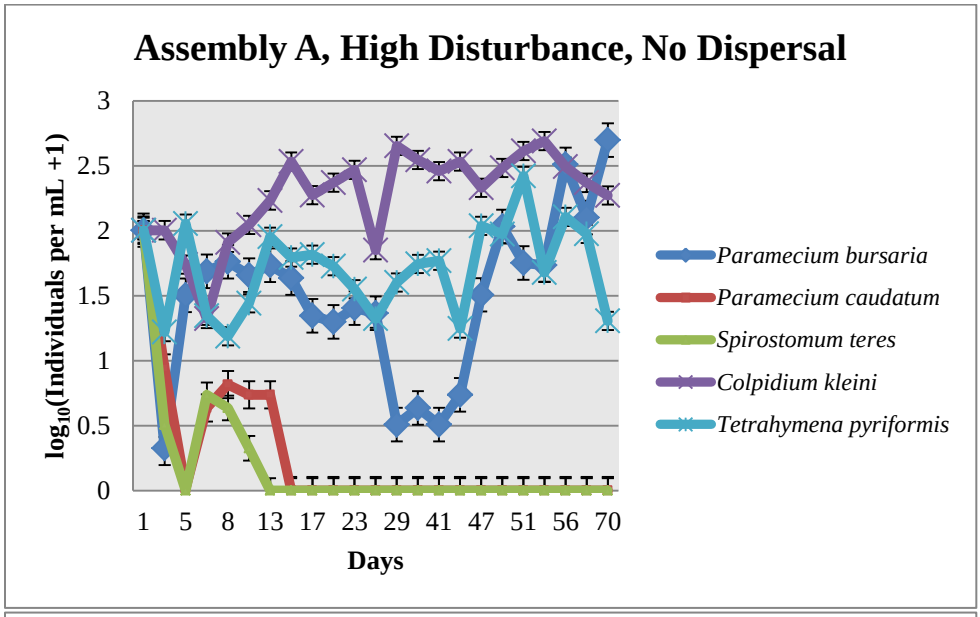
Conclusions

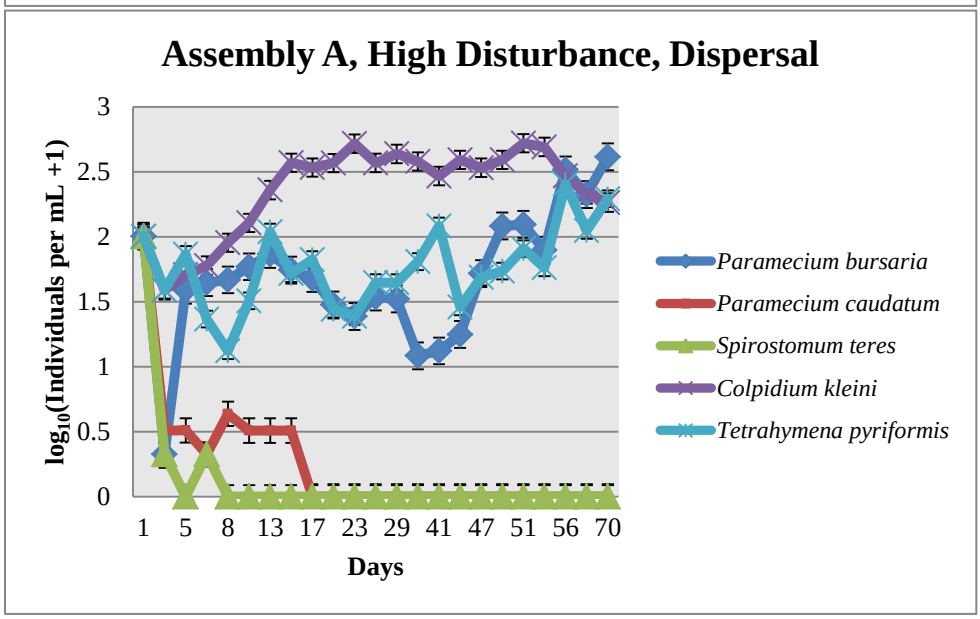
Results of our study show that assembly history has a strong influence on community divergence, but dispersal and disturbance can strongly interact to influence the role of assembly history. Understanding how alternative community states form provides ecologists with predictive power as well as a theoretical framework for restoration of natural habitats (Suding et al. 2004, Temperton et al. 2004, Young et al. 2005). Both theory and experiments of alternative community states have shown that multiple states can exist in the same environmental conditions, implying that simply recreating the original environmental conditions may not necessarily restore ecosystems.

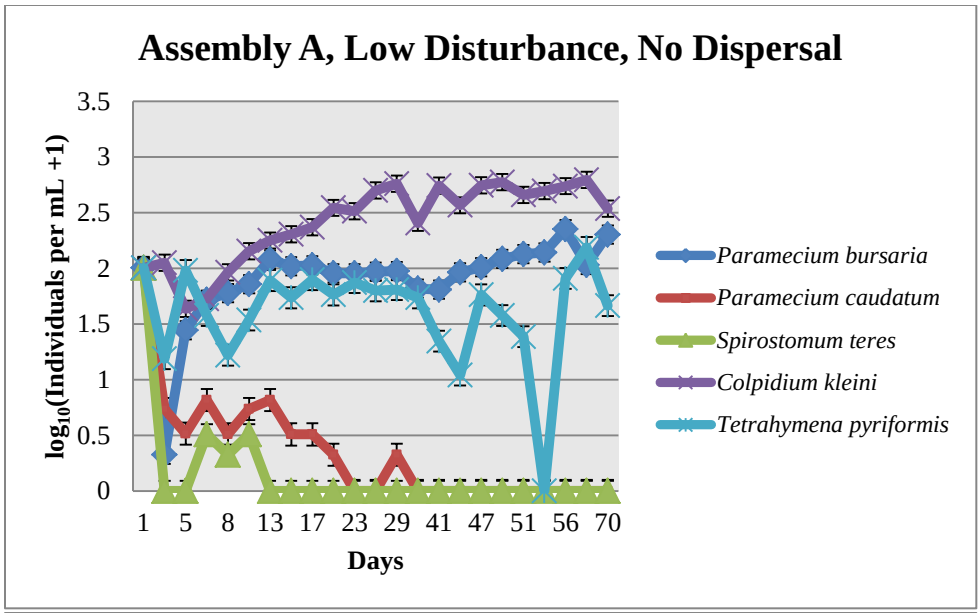
The significant interactive effects of disturbance and dispersal on the role of assembly history in shaping metacommunity assembly, as reported here, further suggest that other, potentially interactive, factors may be considered in order to effectively restore a disturbed habitat.

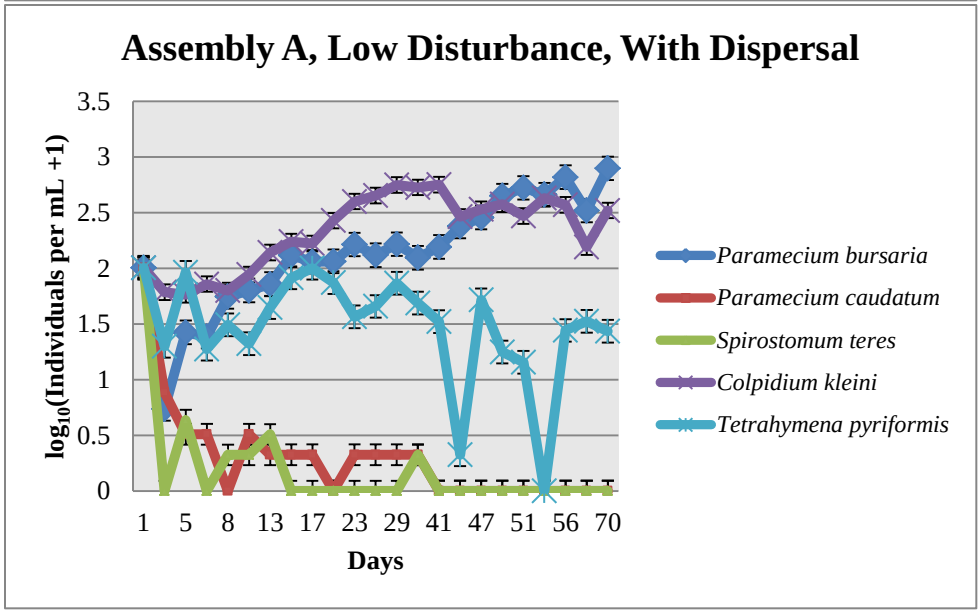
APPENDIX A

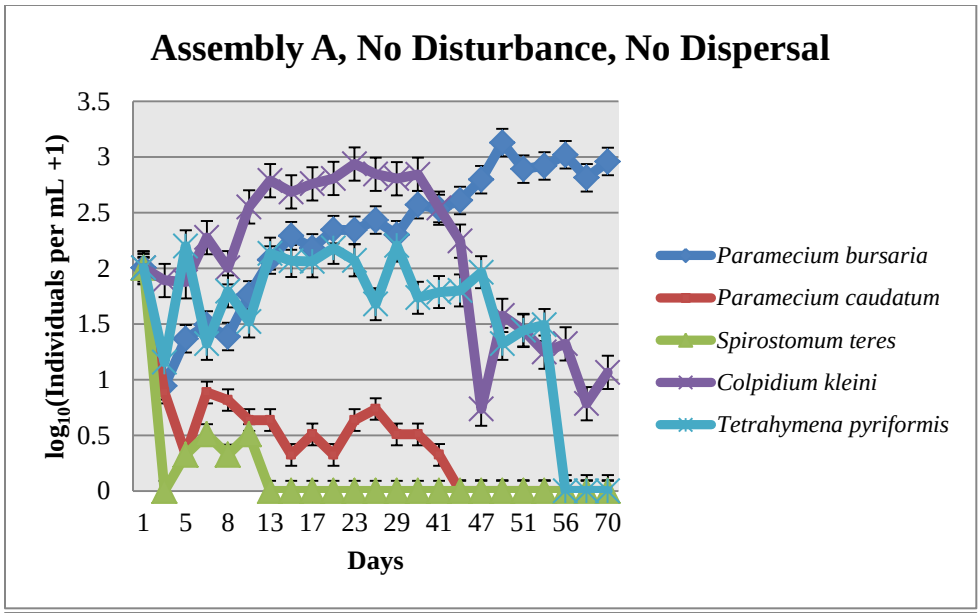
ASSEMBLY HISTORY A ABUNDANCE CURVE

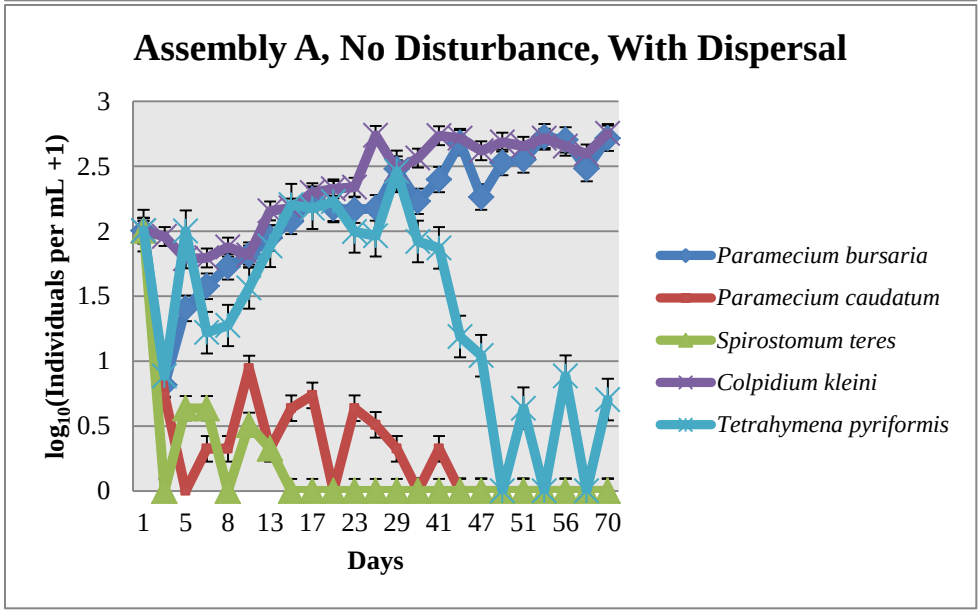


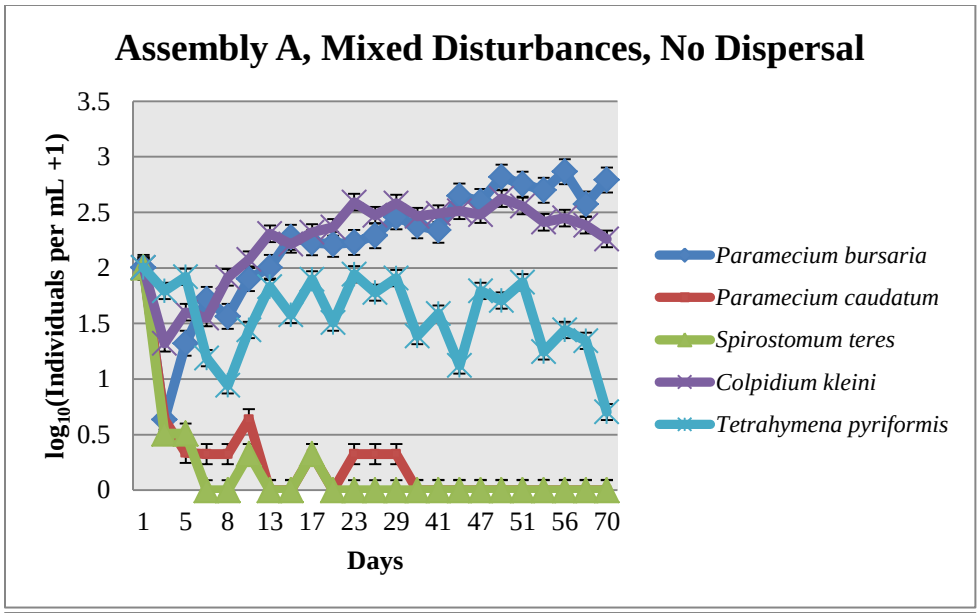



Assembly A, Low Disturbance, No Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly A, Low Disturbance, With Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly A, No Disturbance, No Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly A, No Disturbance, With Dispersal
log10(Individuals per mL +1)
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly A, Mixed Disturbances, No Dispersal
log10(Individuals per mL +1)
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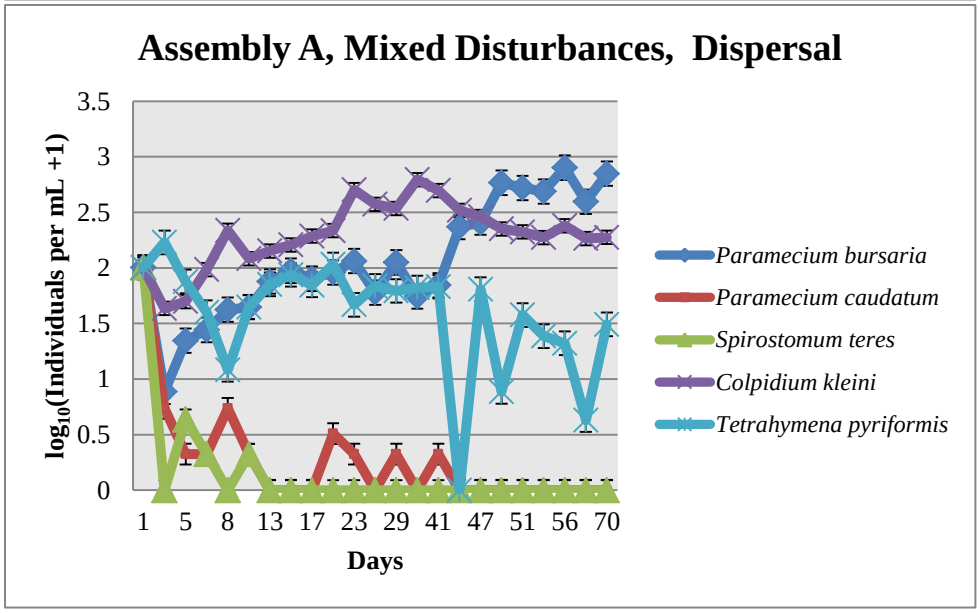
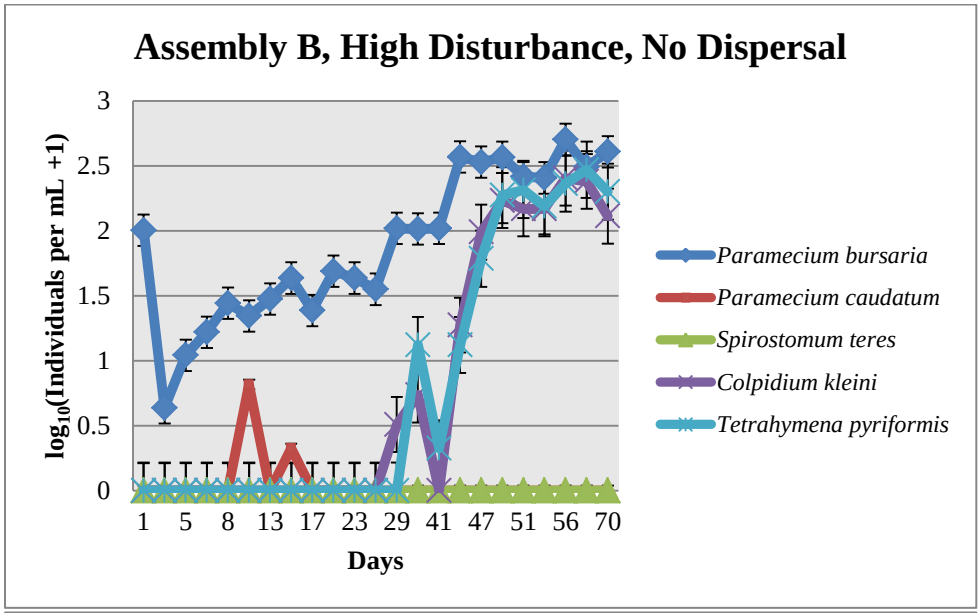
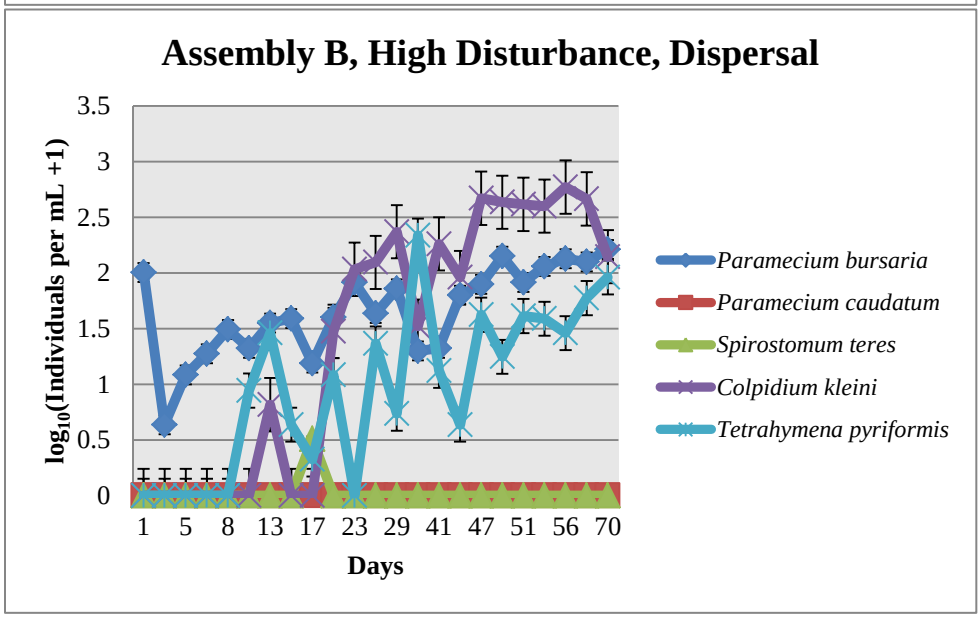
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis

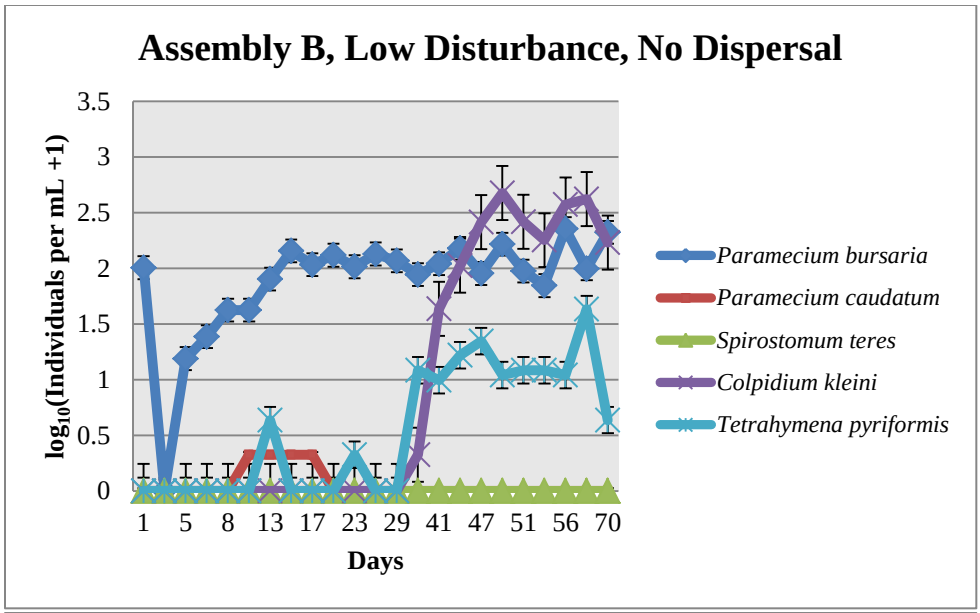

Assembly A, Mixed Disturbances, Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis

APPENDIX B

ASSEMBLY HISTORY B ABUNDANCE CURVES






Assembly B, Low Disturbance, No Dispersal
log10(Individuals per mL +1)
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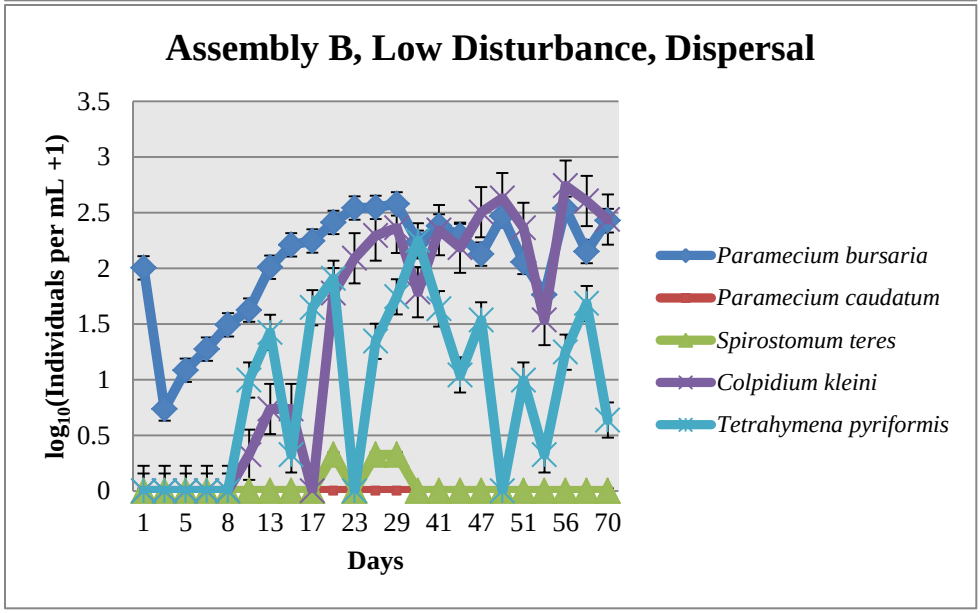
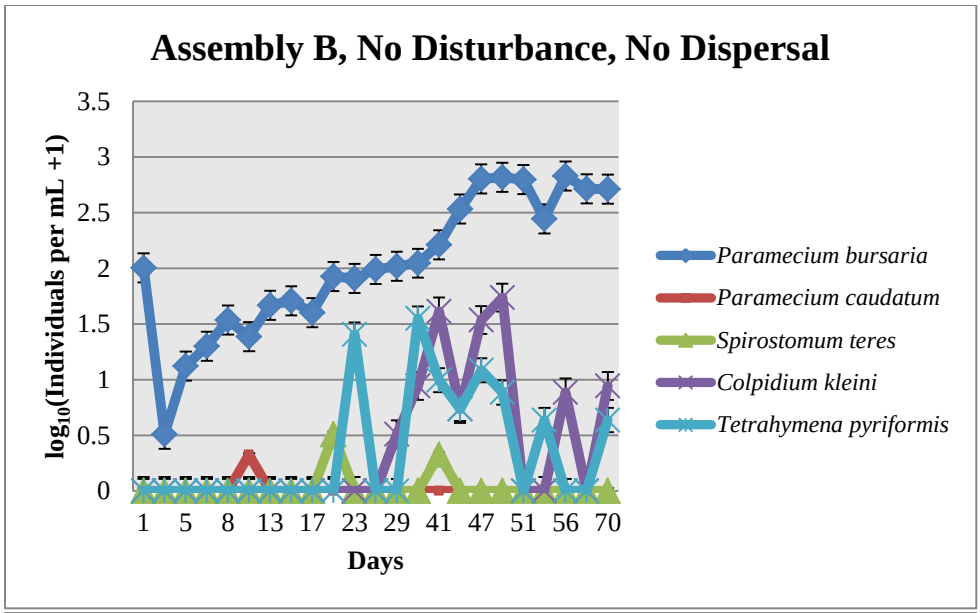
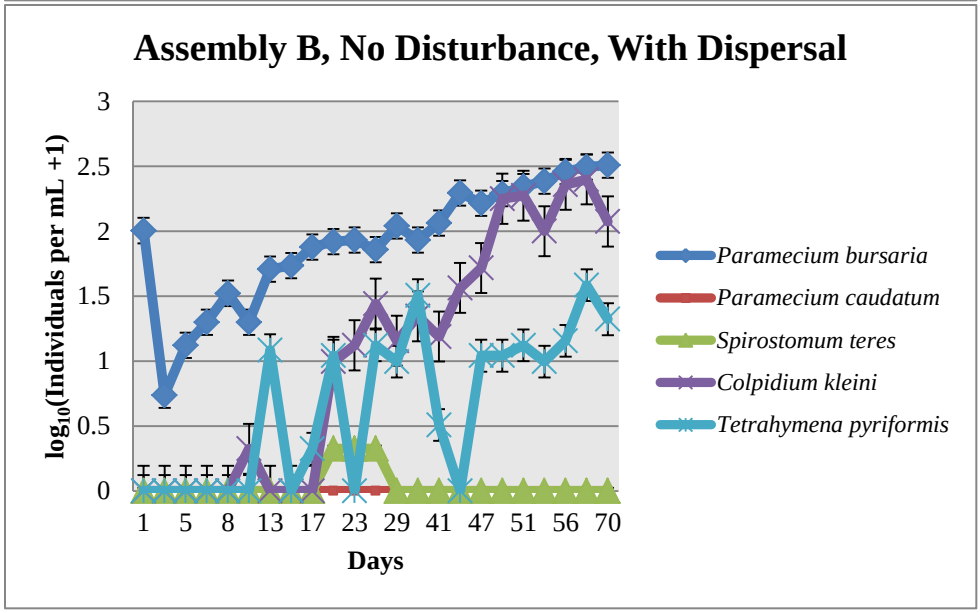
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly B, Low Disturbance, Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly B, No Disturbance, No Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly B, No Disturbance, With Dispersal
log10(Individuals per mL +1)
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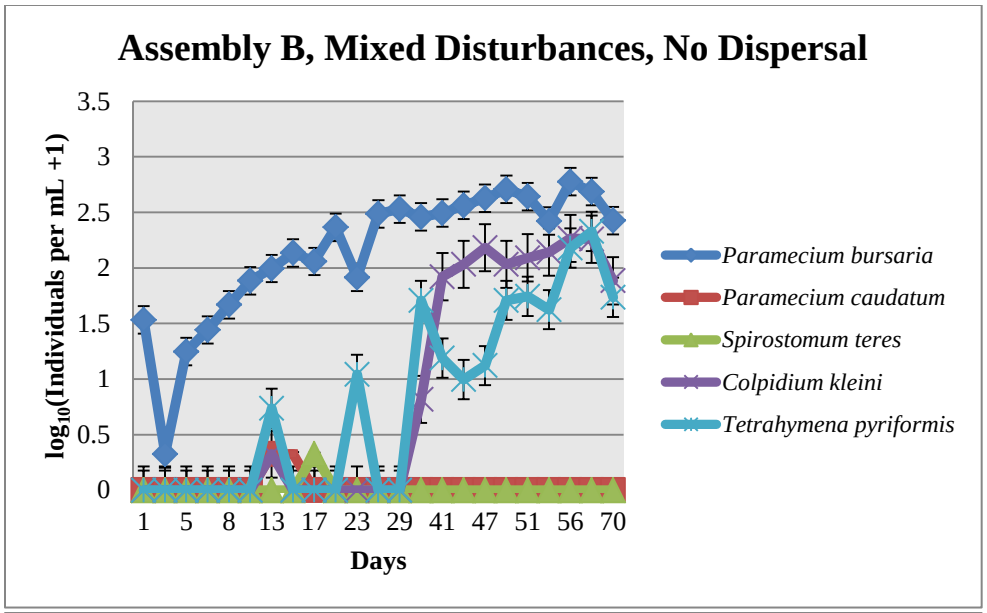
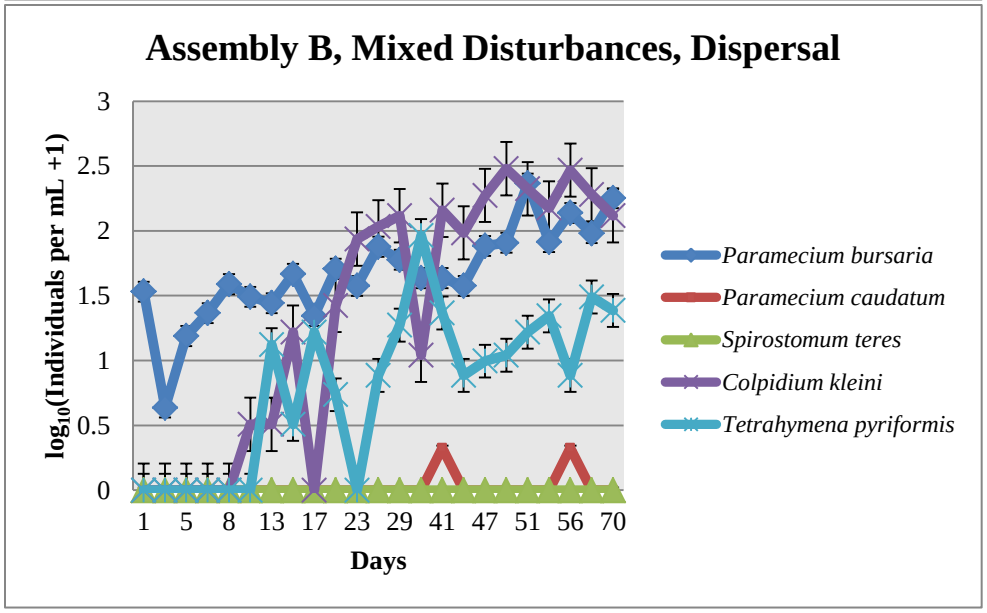
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly B, Mixed Disturbances, No Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly B, Mixed Disturbances, Dispersal
log10(Individuals per mL +1)
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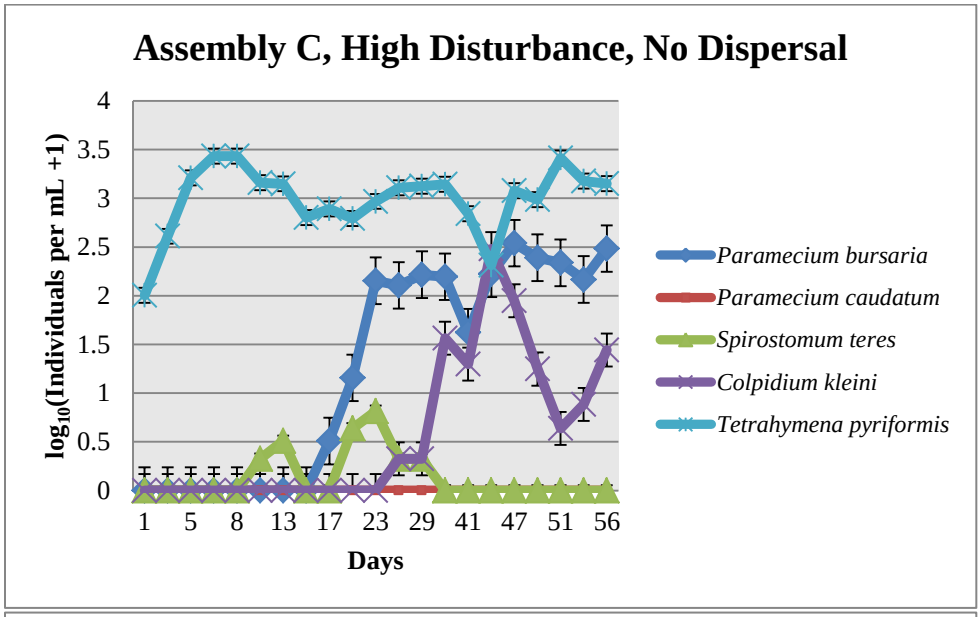
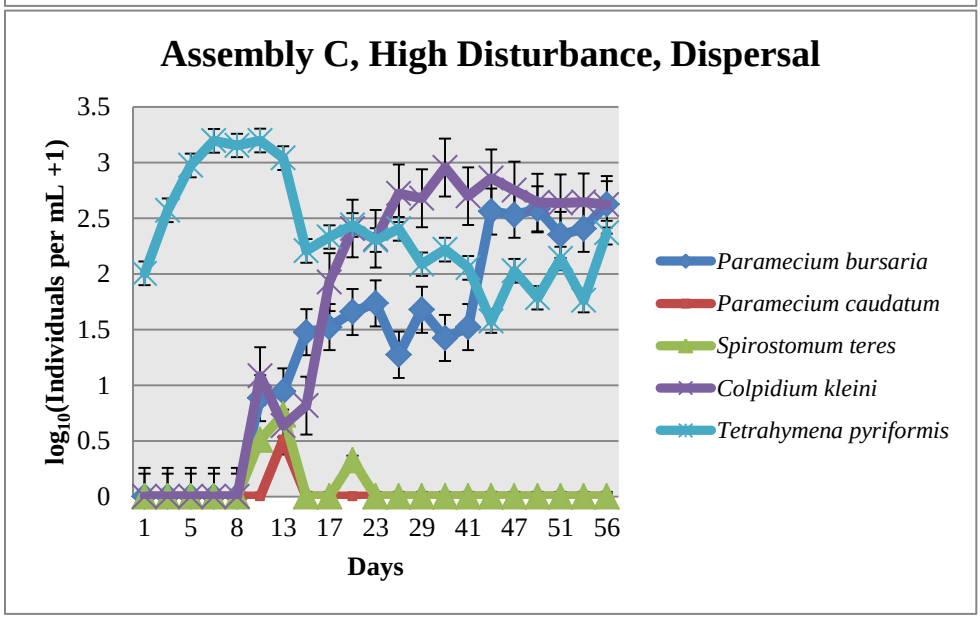
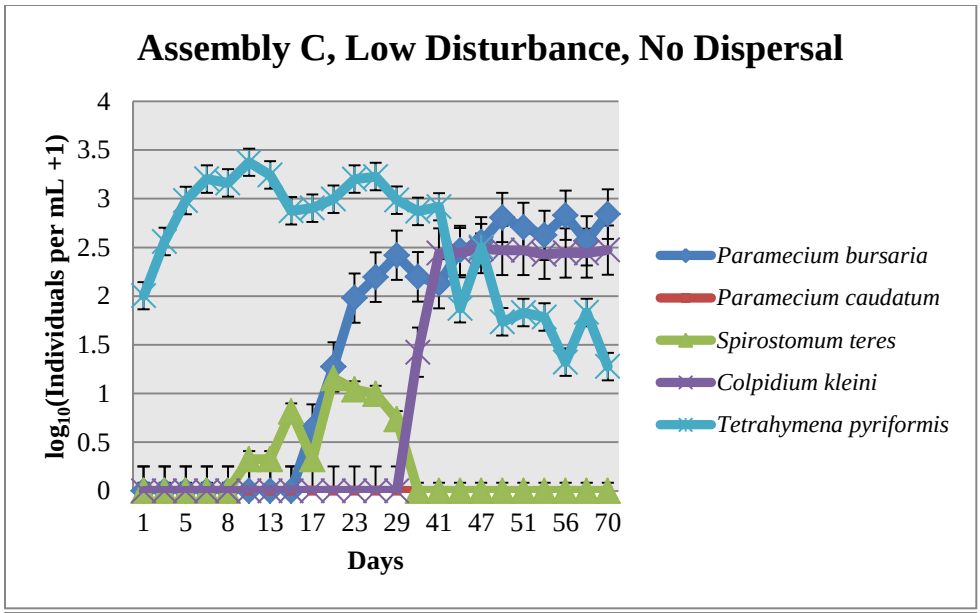
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis

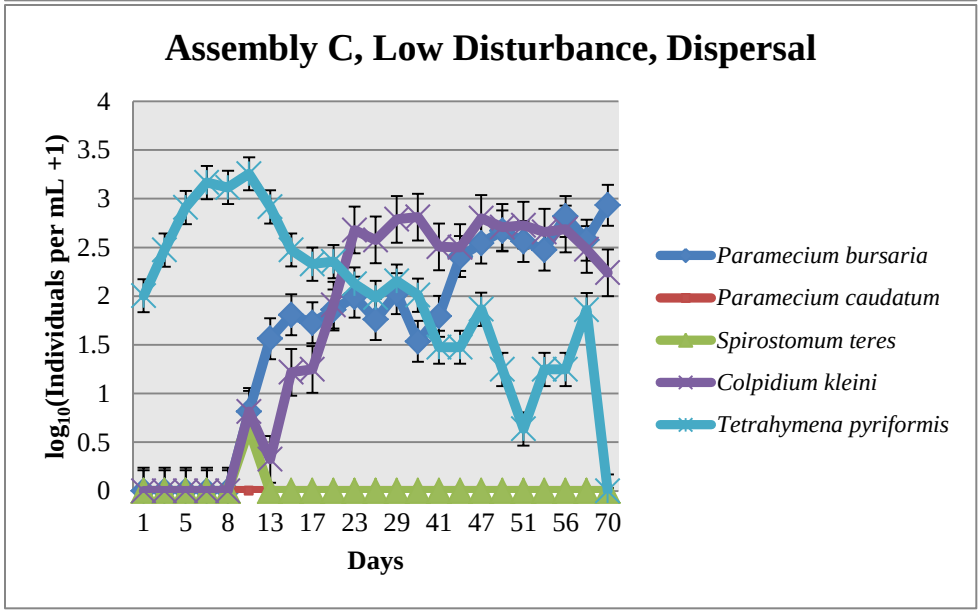
APPENDIX C

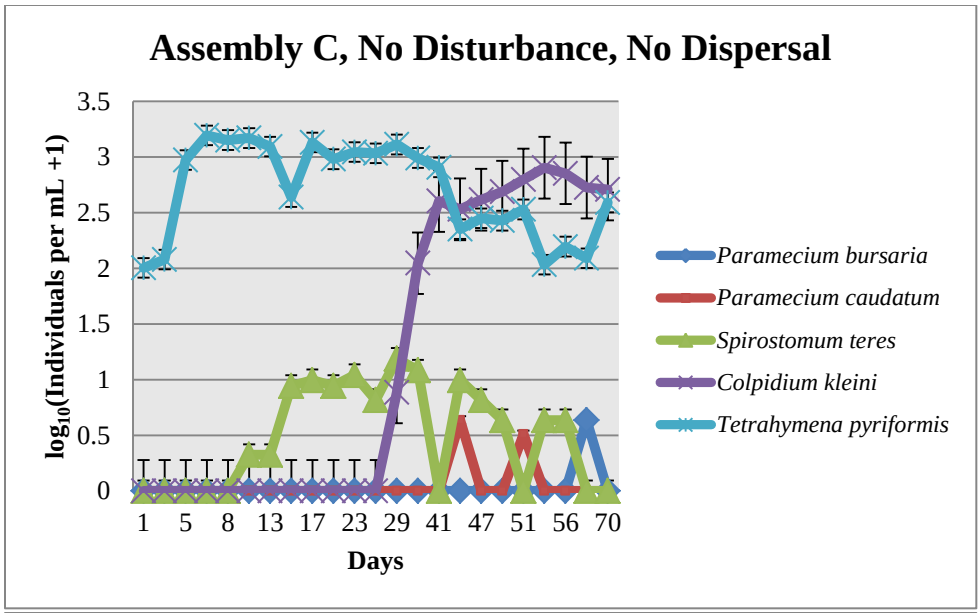
ASSEMBLY HISTORY C ABUNDANCE CURVES

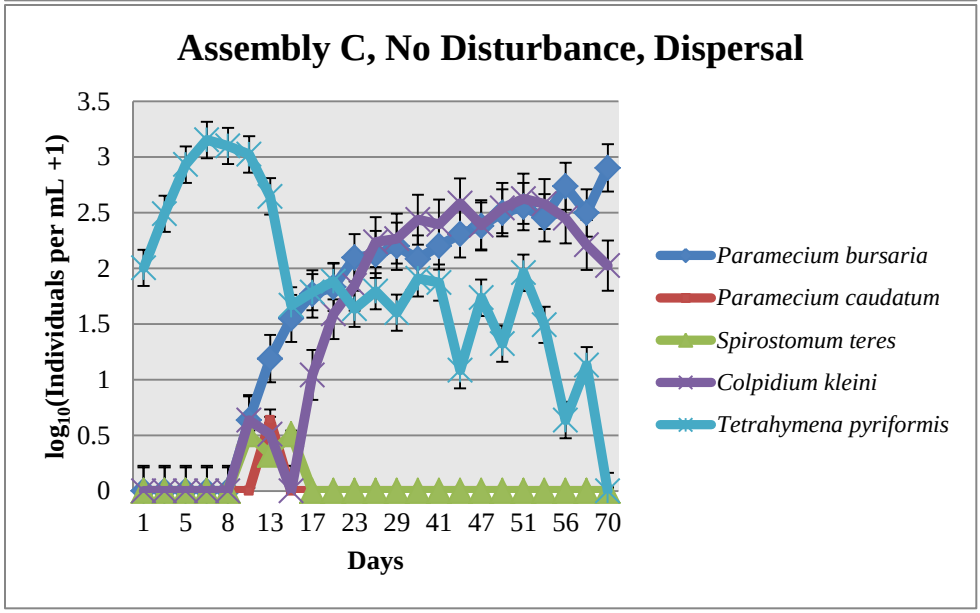


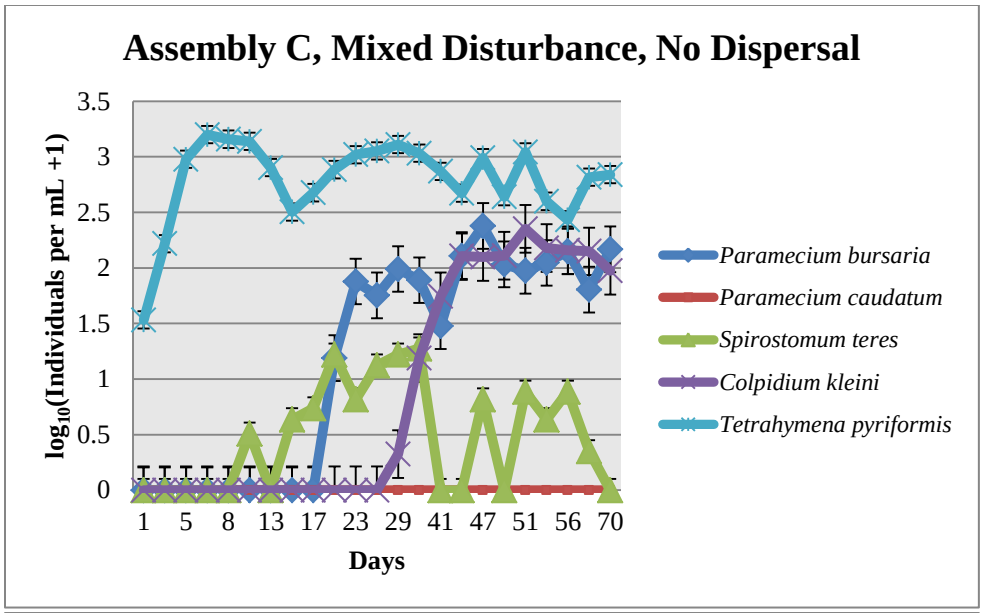


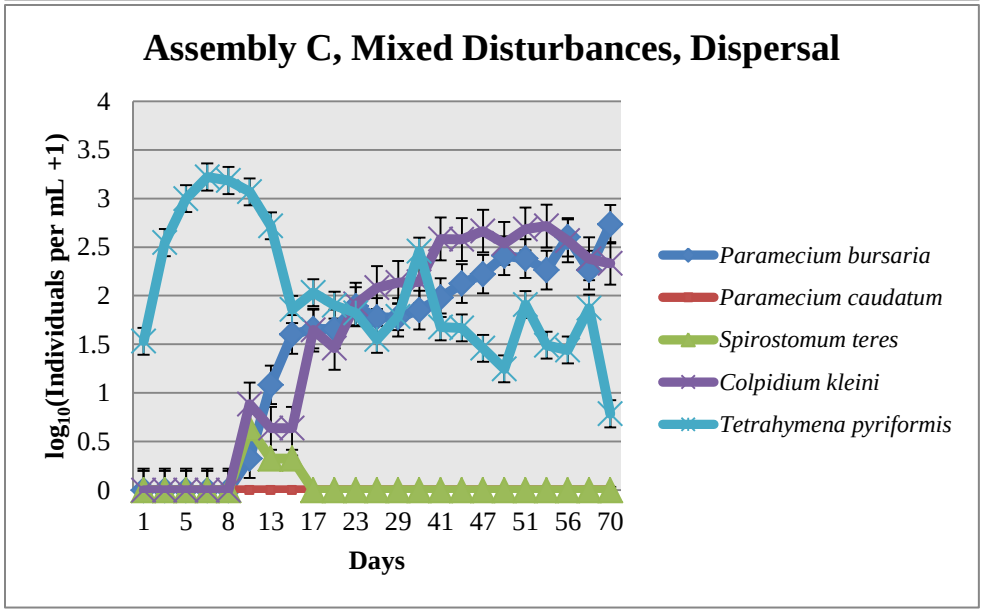

Assembly C, Low Disturbance, No Dispersal
log10(Individuals per mL +1)
4
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly C, Low Disturbance, Dispersal
log10(Individuals per mL +1)
4
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly C, No Disturbance, No Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly C, No Disturbance, Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly C, Mixed Disturbance, No Dispersal
log10(Individuals per mL +1)
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis


Assembly C, Mixed Disturbances, Dispersal
log10(Individuals per mL +1)
4
3.5
3
2.5
2
1.5
1
0.5
0
1 5 8 13 17 23 29 41 47 51 56 70
Days
Paramecium bursaria
Paramecium caudatum
Spirostomum teres
Colpidium kleini
Tetrahymena pyriformis

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